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A fixed energetic ceiling to parental effort in the great tit?

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Summary

1. To elucidate the links between avian brood size, parental effort and parental investment, we measured daily energy expenditure (DEE_{fem}), condition (residuals of mass on tarsus) and feeding rate in female great tits *Parus major L.* rearing broods in which the number of young was either reduced, unmanipulated or enlarged.

2. Female condition was negatively correlated with manipulation when measured at the nestling age of 8 days (measured during the day), which suggests a shift in allocation from self-feeding to chick-feeding. However, there was no detectable manipulation effect on condition measured at the nestling age of 12 days (measured during the night). Either female condition was only affected by manipulation in the early nestling phase or the females adjusted their diurnal mass trajectory in response to brood size manipulation. More detailed data are required to verify this point. There were no indications of a fitness cost associated with the condition during the day, but condition at night was positively related to winter survival. Since manipulation only affected condition during the day, there was no link between manipulation and winter survival.

3. The duration of the working day was not affected by manipulation and female feeding rate tended to flatten off with manipulated brood size. Similarly, brood reduction resulted in a lower DEE_{fem}, whilst brood enlargement had no effect. This suggests that females worked at an energetic ceiling when rearing an unmanipulated brood. However, the level of this 'ceiling' in DEE_{fem} was not fixed: it differed between years. This leads us to conclude that the observed ceiling was imposed by extrinsic factors (e.g. available foraging time) and not by an intrinsic factor such as maximum energy assimilation rate. We hypothesize that time limitation was the cause for the observed ceiling in energy expenditure and that the annual variation in the level of this ceiling was due to annual variation in ambient temperature.

4. A cost of reproduction was previously demonstrated in this population: brood enlargement caused a reduction in the incidence of second clutches. However, since DEE_{fem} did not differ between control and enlarged broods, we judge it unlikely that daily energy expenditure is a general predictor for parental investment.

Key-words: clutch size, condition, energy expenditure, cost of reproduction, parental effort, *Parus major* L.

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Introduction

Parental effort has been defined by Williams (1966) as any behaviour a parent may perform in order to enhance the reproductive value of the offspring of its current reproductive attempt. Parental investment was defined by Trivers (1972) as any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and, hence, reproductive prospects) at the cost of the parent's ability to invest in other offspring. Parental investment is thus the fitness cost incurred through parental effort. The question of how parental effort

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and parental state change with brood size, and whether such changes impose a fitness cost on the parent, is the topic of this paper.

Knowledge of the pathways by which the cost of reproduction arises is important, since it would allow prediction of optimal reproductive strategies under an array of external circumstances. Direct estimation of the fitness cost under many differing circumstances is often not feasible, yet how costs change with these circumstances is crucial to life history theory. In this context, a shortcut to estimate the cost of reproduction would be important. Empirical work on foraging theory, for instance, has profited a great deal from the assumption that maximizing intake rate maximizes fitness, thereby allowing testable predictions of minute to minute foraging behaviour (Tinbergen 1981; Kacelnik 1984). In the case of the cost of reproduction a similar approach can be taken (Daan, Dijkstra & Tinbergen 1990a), provided a causal link between effort and its fitness consequences can be established.

In the current paper we quantify parental effort in the great tit in relation to brood size manipulation (both enlarged and reduced) in terms of energy expenditure, feeding rates and parental condition, and relate these to fitness costs described previously (Tinbergen 1987; Tinbergen & Daan 1990). The relationship between parental effort and brood size *per se* may give us a cue as to what factors limit reproduction, and whether and when fitness costs are likely to occur. A similar approach was taken by Bryant (1988) using data on a number of species, where natural and experimental variation in brood size were lumped for the analysis, because there was no evidence that the response differed. Bryant found only weak evidence for energetic limitation of reproduction and judged that energy expenditure alone will usually be inadequate to indicate prospects for parental survival. The reason that we address the same question again is that we feel that empirical estimates of the parental response to variation in brood size should preferably be based on experimental brood size manipulation, since covariance between the brood size and aspects of individual and/or territorial quality precludes unbiased estimation from correlation (van Noordwijk & de Jong 1986; Grafen 1988). The underlying assumption for these brood size manipulations is that parents will adjust their effort to their new brood size (Lessells 1993). In great tits, parental behaviour is known to be affected by brood size in terms of food provisioning rate (Smith, Källander & Nilsson 1988; Verhulst & Tinbergen 1997), brooding behaviour (Verhulst 1995) and body mass (Smith *et al.* 1987; Lindén 1990).

Many factors may be involved in the causal pathway to a costs of reproduction, including parental energy reserves, parental work rate, risk of predation, risk of infection or risk of an accident. In this study, we emphasize energy- and time-related aspects of effort. Energy is a convenient measure, since it allows the expression of income, capital and expenditure in the same units. Three out of six studies where both brood size was manipulated and parental energy expenditure of the whole animal was analysed (Williams 1987; Dykstra & Karasov 1993; Deerenberg *et al.* 1995; Moreno *et al.* 1995; Verhulst & Tinbergen 1997; Wright *et al.* 1998), reported a manipulation effect on energy expenditure. In this study we consider three causal pathways concerning energy and time that may apply. Future reproductive prospects of the parent may be affected by effort through effects of (1) the energy reserves or (2) the energy turnover of the parent. Furthermore, there is the possibility that the cost of reproduction is not caused by the state of the parent, but by (3) the state of the brood. If parents are limited somehow in their behaviour, and the amount of food brought to the nest does not increase proportionally to the needs of the brood, chicks may grow more slowly and need longer care. A conflict may then arise between raising a first and a subsequent clutch within a season (Tinbergen 1987; Smith *et al.* 1987; Lindén 1988; Verhulst, Tinbergen & Daan 1997; Verhulst & Hut 1996).

Methods

Data were collected in the years 1983–87, in the Hoge Veluwe in the Netherlands. The Hoge Veluwe is a mixed wood on poor soil with intermediate breeding densities of great tits (van Balen 1973). Nest boxes were checked once a week. Around expected hatching date checks were done once every day or two in order to establish hatching date.

LARGE DATA-SET

Brood size manipulation was performed the second day after hatching. In the years 1983–87, triplets of nests with approximately the same clutch size and hatching date were selected, and half of the young from one nest were transferred to a second nest, while a third was kept unmanipulated as a control. In total, 348 first broods were included in the experiment (referred to as the large data set). Fitness consequences of these manipulations have been described elsewhere (Tinbergen 1987; Tinbergen & Daan 1990).

The fate of the broods was followed by weekly nest box checks. In addition, nestlings were ringed around day 8 (range days 6–9, referred to as day 8),

usually caught between 8.00 and 12.00 h), and parents were caught using spring traps, weighed, measured and, if necessary, ringed. Nestling body mass and tarsus were taken at the age of 14 days (hatching day = day 0). Females were again caught at nestling age of around day 12 (range day 9–15, referred to as day 12). In this case, the birds were taken in the night (between 23.00 and 02.00 h) while roosting with the brood. The number of fledged young was estimated by correcting the number of young at day 14 for dead chicks or rings found in the nesting material after fledging. Both nestling and parental condition were taken as the residual of the body mass vs. tarsus regression, and is given in grams. The regression of female mass on tarsus on day 8 [female mass (g) = 7·514 + 0·5138*tarsus (mm), $R^2 = 0{\cdot}138$] was used to calculate female condition for all nestling ages as the difference between her body mass and this regression line. The relationship between body mass and tarsus did not differ between years (ANCOVA, year effect NS, year × tarsus NS). For females no effect of time of day on body mass existed within the daylight or the night period (both $P > 0{\cdot}2$). For males the body mass did depend positively on the time of day ($b = + 0{\cdot}109$ g h^{-1}) and condition was calculated for 11.00 h [male mass (g) = 6·229 + 0·5791*tarsus (mm)].

The average tarsus length of the females (mean = 19·68 mm, SE = 0·04, $n = 267$) did not differ between years, or between manipulation categories (ANOVA). Male tarsi (mean 20·10, SE = 0·04, $n = 219$) differed significantly between years and the males of the reduced group had longer tarsi than those of the enlarged group (Tukey pair wise comparison $P < 0{\cdot}05$), which made us analyse condition (residuals of body mass on tarsus) as a state variable, rather than body mass.

The probability of having a second clutch was determined by reading colour rings of the females during incubation of the second clutch or by catching the parents during their second nestling phase. Local survival was estimated on the basis of recaptures of the breeding birds during the next breeding season in the study area. Of the breeding birds, 92% of the females and 77% of the males were identified (Tinbergen & Daan 1990).

RESTRICTED DATA-SET

In order to measure behavioural differences between birds tending manipulated broods, we studied a subsample of 38 pairs in more detail, referred to as the restricted data set. The emphasis was laid on the females because they roost in the nest box and can be caught readily.

To monitor feeding rate, switches were attached to the nest box opening. Registration of the feeding rate was on a time base, allowing an estimate of the duration of the active period (time between first and last visit to the nest). Observations were done to check the accuracy of the switches and, on the sample day (nestling age of 11 or 12 days), to estimate female share in the visits on two or three periods, each of two hours.

Food availability was measured using 6–10 caterpillar frass collectors of 0·25 m^2 in the vicinity of the nest box where DEE_{fem} was measured (10–50 m, depending on the location of the main food trees). Frass was collected over a 2-day period starting the day before the DLW measurements. In total, 224 measurements could be used. Frass was dried, cleaned and converted to caterpillar biomass using a temperature correction (Tinbergen & Dietz 1994).

The Daily Energy Expenditure ($DEE_{fem,}$ kJ per 24 h) of female great tits was measured at nestling age of 11 or 12 days using the doubly labelled water (DLW) technique as described in Tinbergen & Dietz 1994. Normally, the DEE of three females was measured simultaneously, one in each experimental category. The females were caught at night in the nest box and recaptured after 24 h, again in the nest box. We measured 38 females over 3 years (1985, 1986 and 1987). DEE_{fem} was corrected for the proportion of night-time hours between the initial and final sample following Tinbergen & Dietz (1994).

Of 38 females, 10 did not sleep in the box the second night of the DLW sampling period and could thus not be recaptured the following night. They were recaptured the next morning and, consequently, the sampling period was substantially longer than 24 h. Although the probability of roosting in the box was independent of manipulation category (logistic regression $\chi^2 = 0{\cdot}6457$, d.f. = 2, $P > 0{\cdot}7$), we expected potential biases, generated through variation in energetic costs during the night and through differences in water balance. Indeed, a preliminary analysis suggests that the DEE_{fem} of these 10 birds was affected more strongly by the ambient temperature (mean over 24 h) than the DEE_{fem} of the other birds (Fig. 1). In order to judge whether this could affect our conclusions, we checked all our analyses by (i) repeating the analysis for the birds that were caught both nights in the nest box ($n = 28$), and (ii) by correcting for the difference in temperature effect according to the regression given above ($n = 38$). Our conclusions were not affected by this strategy of data analysis, and we present only the analysis based on all 38 points.

When we tested for effects of manipulation we used regression with an ordered variable where reduced = 1, control = 2 and enlarged = 3, and tested for curvy-linearity by including the squared manipulation as an explanatory variable. We used ANOVAs to verify whether means between the

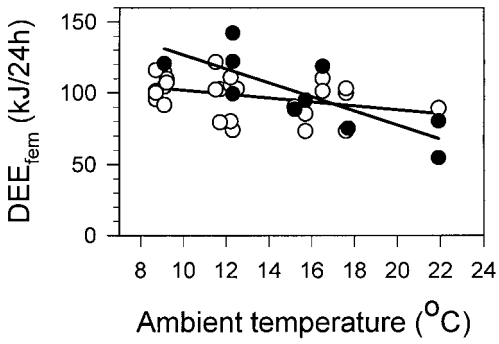

Fig. 1. Daily energy expenditure of female great tits (DEE_{fem}) in relation to ambient temperature for two different groups: ○, both nights in the nest box; ●, only first night in the nest box. An ANCOVA showed the difference between the slopes to be significant (interaction between ambient temperature and a dummy variable indicating whether a female spent the second night in the nest box: $F_{1,34} = 7{\cdot}207$, $P < 0{\cdot}02$).

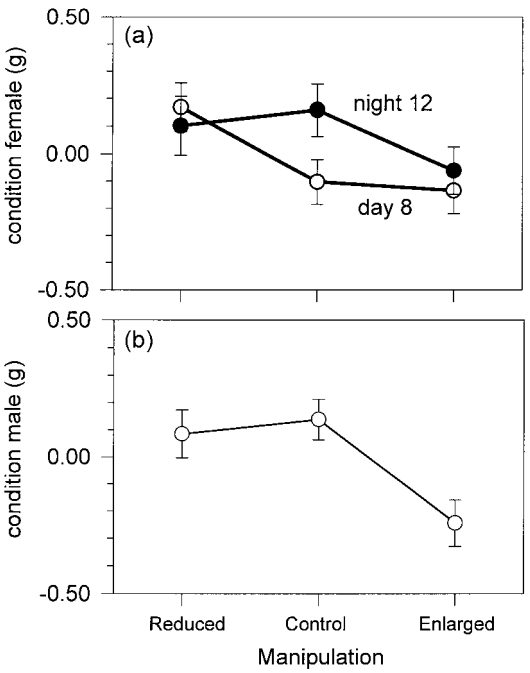

Fig. 2. Body condition calculated as the residuals of mass around day 8 on tarsus length. (a) Female condition (± SEM) around nestling age 8 taken during the day (○, the reduced group differed significantly from the enlarged, Tukey $P = 0{\cdot}05$) and around nestling age 12 taken during the night (●) as a function of manipulation. (b) Male condition (± SEM) around nestling age 8 taken during the day (○, the enlarged group differed significantly from both the reduced and the control group, Tukey $P = 0{\cdot}05$).

manipulation categories differed. All tests were two-tailed, with significance accepted at $P < 0{\cdot}05$.

Results

PARENTAL STATE AND BEHAVIOUR

Condition

Condition of females was negatively related to manipulation when measured at day 8 ($b = -0{\cdot}138$ g per manipulation, $F_{1,226} = 5{\cdot}41$, $P < 0{\cdot}03$, Fig. 2a; ANCOVA using the large data set, controlled for nestling age) and did not differ between years. No significant quadratic effect of manipulation existed ($F_{1,225} = 1{\cdot}61$, $P > 0{\cdot}2$). In contrast, the condition of females at day 12 (night-time captures) was not significantly related to manipulation, nor its square (Fig. 2a; manipulation: $F_{1,178} = 1{\cdot}706$, $P > 0{\cdot}19$; manipulation squared $F_{1,177} = 0{\cdot}898$, $P > 0{\cdot}34$, controlled for year), but differed between years ($F_{4,179} = 5{\cdot}35$, $P < 0{\cdot}001$). In agreement with these results, the within female daily mass change between days 8 and 12 was affected by manipulation (ANOVA, $F_{2,163} = 5{\cdot}14$, $P < 0{\cdot}01$, Fig. 2a). Pair-wise comparisons showed that the mass change in the reduced group was significantly different from that of the control group (Tukey $P < 0{\cdot}05$), but not from the enlarged group, nor was there a significant difference between the enlarged and control group. A further contrast between the day 8 and 12 measurements was that condition around day 8 was dependent on nestling age ($b = -0{\cdot}224$ g day^{-1}, SEM $= 0{\cdot}054$, $F_{1,226} = 17{\cdot}43$, $P < 0{\cdot}0001$, controlling for manipulation), whilst the condition around day 12 was not ($b = -0{\cdot}030$ g day^{-1}, SEM $= 0{\cdot}051$, $F_{1,178} = 0{\cdot}349$, $P > 0{\cdot}5$).

Condition of males was also negatively related to manipulation at day 8 ($b = -0{\cdot}160$ g per manipulation, $F_{1,216} = 6{\cdot}49$, $P < 0{\cdot}02$, Fig. 2b; ANCOVA using the large data set, controlled for nestling age) and did not differ between years. No significant quadratic effect of manipulation existed ($F_{1,215} = 1{\cdot}53$, $P > 0{\cdot}21$).

Working day

The duration of the active period may affect energy expenditure (Sanz *et al.* 1998). However, working day was neither dependent on manipulation, nor on date (both $P > 0{\cdot}1$, Table 1). On average a working day was 15·7 h (SD $= 0{\cdot}79$, $n = 30$), close to the value reported for the study population on Vlieland (Verhulst & Tinbergen 1997).

Feeding rate

The daily number of feeding visits of the female increased with manipulation (Visits $= 35{\cdot}24 + 95{\cdot}45 \times$ manipulation, $P = 0{\cdot}001$, $R^2 = 0{\cdot}26$,

Table 1. Parameters on the brood size and female behaviour in relation to manipulation

	Manipulation								
	Reduced			Control			Enlarged		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Brood size	5·3	0·8	13	9·0	1·9	14	14	2·14	11
Activity (h/24 h)	15·5	0·8	10	15·6	0·8	12	16·05	0·71	9
Share female (fraction)	0·49	0·19	11	0·48	0·12	14	0·48	0·07	11
Female visits (*n*/24 h)	124·8	75·5	13	238·0	105·7	13	313·9	194·0	10
DEE (kJ/24 h)	88·7	11·7	13	102·1	17·4	14	105·5	18·5	11
DEE/g [kJ/(g*24 h)]	5·09	0·59	13	5·65	0·88	14	6·28	0·91	11
Female mass (g)	7·38	0·77	13	18·01	0·59	14	17·49	0·97	11

restricted data set) and did not differ between years ($F_{2,32} = 1{\cdot}44$, $P > 0{\cdot}23$). Feeding rate of the enlarged and the reduced group differed significantly (Tukey pair-wise comparison, $P < 0{\cdot}05$), but neither of these differed significantly from the control group. However, variances differed significantly between the three groups (Bartletts test $\chi^2 = 9{\cdot}75$, d.f. $= 2$, $P < 0{\cdot}01$) and this was due to one female with an exceptionally high feeding rate (Figs 3a and 5). From the observations we know that she exploited one oak tree, at some distance from the nest, with an exceptionally high density of small caterpillars of the winter moth (*Operophtera brumata*), and this particular bird spent a very high proportion of her time flying. If we excluded this bird, feeding rate tended to level off with increasing manipulation (reduced 125, control 238, enlarged 255 visits per day). Although manipulation squared was not significant ($F_{1,32} = 1{\cdot}62$, $P > 0{\cdot}20$) the reduced group had significantly lower feeding rates than the enlarged and the control, while the latter two did not differ from each other (ANOVA, Tukey pair-wise comparison, $P < 0{\cdot}05$). We conclude that females rearing enlarged broods do not increase their feeding rate proportionally, although the data on the one excluded female suggest they may be able to do so in exceptional circumstances.

The share of the female in provisioning the nest was neither related to manipulation, nor different between years, implying that the trends in feeding visits with manipulation were similar for males and females (Table 1). Average female share was 0·49 (SD $= 0{\cdot}13$, $n = 36$).

Energy expenditure

Controlling for year, DEE_{fem} was significantly related to manipulation and its square (Fig. 4; year: $F_{2,33} = 11{\cdot}18$, $P < 0{\cdot}001$; manipulation: $F_{1,33} = 7{\cdot}39$, $P < 0{\cdot}01$; manipulation squared: $F_{1,33} = 4{\cdot}859$, $P < 0{\cdot}05$). No additional effect of the original brood size could be detected. In a pair-wise comparison of experimental categories, DEE_{fem} (controlled for year) in the reduced group differed significantly from both the control and the enlarged (Tukey, $P < 0{\cdot}05$, see also Table 1), while the latter two groups were indistinguishable. This is an important result, since it points at a ceiling to energy expenditure during parental care as suggested by Drent & Daan (1980). When the data are plotted for each year separately (Fig. 4), the year specific level of this 'ceiling' is shown. We conclude that, within years, DEE_{fem} levelled off with manipulated brood size and the level of this energetic ceiling differed between years.

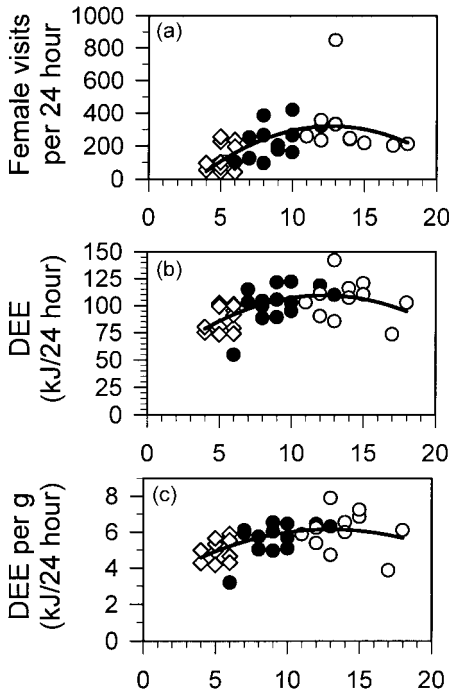

Fig. 3. Female behaviour in relation to the actual number of young after manipulation (MY) and its square (MY^2) at nestling age of 12 days. Symbols denote manipulation categories (reduced: ◇ control: ●; enlarged: ○). (a) Female feeding visits per day (visits $= -261{\cdot}1 + 91{\cdot}1$*MY $- 3{\cdot}58$* MY^2, both $P < 0{\cdot}02$, $R^2 = 0{\cdot}35$) (b) Female daily energy expenditure ($DEE_{fem} = 41{\cdot}2 + 11{\cdot}1$*MY $- 0{\cdot}452$*MY^2, both $P < 0{\cdot}02$, $R^2 = 0{\cdot}32$) (c) DEE_{fem} per gram body mass. ($DEE_{fem}/BM = 2{\cdot}86 + 0{\cdot}506$*MY-$0{\cdot}019$*$MY^2$, $P < 0{\cdot}05$, $R^2 = 0{\cdot}28$).

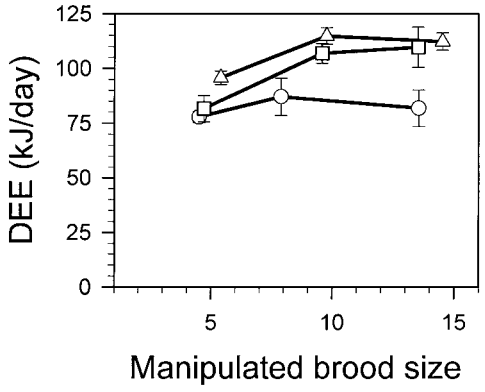

Fig. 4. Mean DEE_{fem} (± SEM) of females tending manipulated broods. ○, 1985; △, 1986; □, 1987 plotted against the mean number of young in the nest directly after manipulation.

What could explain the annual variation in the energetic ceiling? Tinbergen & Dietz (1994) previously showed that variation in DEE_{fem} among females rearing unmanipulated first or second broods was best explained with a regression model including feeding rate, ambient temperature, female body mass and caterpillar abundance (the main food supply). When this analysis was repeated for the restricted data set temperature and feeding rate remained significant (Fig. 5). The direction of the non-significant effects of female body mass and caterpillar biomass were consistent with the earlier analysis. Temperature and feeding rate independently explained a large proportion of the variation in DEE_{fem} (29 and 27%, respectively). When these two explanatory variables were included in the model, no additional significant year effect could be shown ($F_{2,31} = 1{\cdot}708$, $P > 0{\cdot}19$). To identify the factor causing the annual variation in DEE_{fem}, we tested the significance of the year factor in models from which one of the explanatory variables was excluded. The exclusion of temperature yielded a significant year effect ($F_{2,32} = 8{\cdot}554$, $P < 0{\cdot}005$), while exclusion of the feeding visits did not ($F_{2,32} = 0{\cdot}818$, $P > 0{\cdot}44$). In agreement with this finding, mean temperature on the sampling day differed greatly between years (1985: 18·5°C, SD 2·7, $n = 9$; 1986: 11·1°C, SD 3·0, $n = 15$; 1987: 12·6°C, SD 2·0, $n = 14$; ANOVA: $F_{2,35} = 23{\cdot}41$, $P < 0{\cdot}001$), but as mentioned above no difference in the daily number of feeding visits existed between years. We conclude that the annual variation in the energetic ceiling was likely to be due to differences in ambient temperature.

STATE EFFECTS ON FITNESS?

Here, we analyse associations of parental and brood state with the cost of reproduction. As previously described (Tinbergen 1987; Tinbergen & Daan 1990), the costs of reproduction in our study area are due to a change in the probability of producing a second clutch. A more detailed re-analysis of the data using multiple logistic regression (large data set, subset of birds that produced at least one fledgling) shows that the probability of a second clutch differed between years ($\chi^2 = 20{\cdot}00$, d.f. $= 4$, $P < 0{\cdot}001$), and was negatively associated with hatch date of the young ($\chi^2 = 8{\cdot}91$, d.f. $= 1$, $P < 0{\cdot}005$) and manipulation ($\chi^2 = 14{\cdot}44$, d.f. $= 1$, $P < 0{\cdot}001$, deviance final model: 308·24, d.f. $= 266$). Manipulation squared did not reduce the deviance significantly ($\chi^2 = 0{\cdot}02$, d.f. $= 1$, $P > 0{\cdot}88$). When the effects of reducing and enlarging the brood were tested separately (controlled for hatch-date and year), the birds rearing enlarged broods differed just not significantly from the control group ($\chi^2 = 3{\cdot}79$, d.f. $= 1$, $P < 0{\cdot}052$, $b = -0{\cdot}71$) and the controls were just not significantly different from the reduced group ($\chi^2 = 3{\cdot}03$, d.f. $= 1$, $P = 0{\cdot}082$, $b = -0{\cdot}56$). The difference between reduced and enlarged was, however, highly significant ($\chi^2 = 14{\cdot}45$, d.f. $= 1$, $P < 0{\cdot}001$). The manipulation

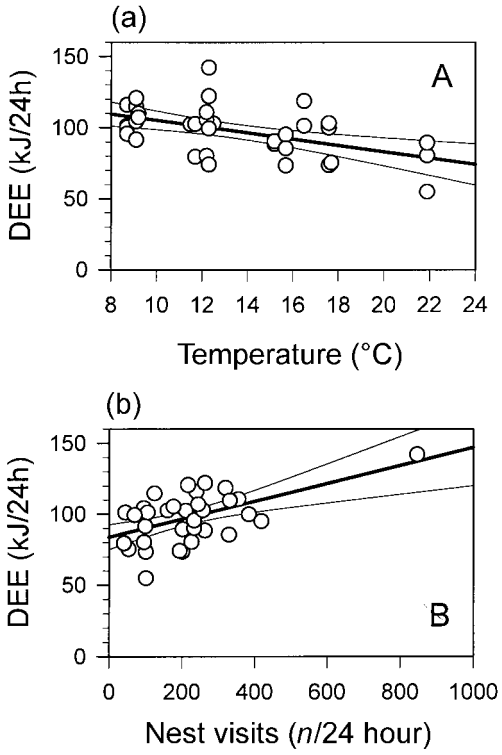

Fig. 5. Effects on DEE_{fem} of (a) ambient temperature (°C) (b) female feeding rate (feeds/day). Simple regression lines and 95% confidence intervals are shown. Full regression model: constant = 114·5; temperature: $b = -2{\cdot}37$, $t = -4{\cdot}91$, $P < 0{\cdot}001$; feeding rate: $b = 0{\cdot}067$, $t = 5{\cdot}17$, $P < 0{\cdot}001$; adjusted $R^2 = 0{\cdot}57$, $n = 36$.

effects on the probability of having a second clutch are thus symmetrical.

Parental state and behaviour

None of the different measures of parental condition was significantly associated with the probability of a second clutch (male day 8: $\chi^2 = 0{\cdot}20$, d.f. $= 1$, $P > 0{\cdot}9$; female day 8: $\chi^2 = 0{\cdot}36$, d.f. $= 1$, $P > 0{\cdot}5$; female night 12: $\chi^2 = 1{\cdot}30$, d.f. $= 1$, $P > 0{\cdot}2$, controlled for year and hatch date, large data set, *n*, respectively, 194, 201 and 170, for results in the restricted data set see Table 2). A causal relationship between condition and the cost of reproduction seems therefore unlikely.

Feeding rate was negatively associated with the probability of producing a second clutch (Table 2, restricted data set), and the association with DEE_{fem} approached significance, which suggests a direct effect of work on the costs of reproduction. However, DEE_{fem} cannot cause the cost of reproduction, because it did not differ between control and enlarged broods (Fig. 4), while brood enlargement decreased the probability of a second clutch. One could argue that the rejection probability should be lowered due to multiple comparisons. According to the Dunn–Šidák method the rejection probability should be adjusted to around $P < 0{\cdot}006$, leading to the conclusion that the probability of a second clutch was neither explained by feeding rate nor by DEE_{fem}.

The duration of the working day was not associated with the probability of a second clutch (Table 2). For those birds that did produce a second clutch, the interval between the first and second clutch (another parameter affected by brood size manipulation in our population, Tinbergen 1987), was not related to DEE_{fem} ($F_{1,15} = 0{\cdot}02$, $P > 0{\cdot}89$) or feeding rate ($F_{1,14} = 0{\cdot}02$, $P > 0{\cdot}89$).

Brood state

The state of the brood could affect the probability of a second clutch via interference with a second clutch (Smith *et al.* 1987; Tinbergen 1987; Verhulst & Hut 1996; Verhulst *et al.* 1997). Effects of brood size manipulation on the nestling number and state have been described earlier for this population (Tinbergen 1987; Tinbergen & Daan 1990). In brief, the probability to fledge at least one young differed between years ($\chi^2 = 53{\cdot}03$, d.f. $= 4$, $P < 0{\cdot}001$), but was independent of manipulation category ($\chi^2 = 2{\cdot}06$, d.f. $= 2$, $P > 0{\cdot}35$, $n = 348$ nests). Nestling mortality for the remaining nests increased with manipulated brood size, but the number of fledglings remained positively related to manipulation, and differed significantly in each pair-wise combination among the three manipulation cate-

Table 2. Associations between the behaviour during the current reproductive event and the subsequent probability of a second clutch. Logistic regressions on one explanatory variable at a time and controlling for year. The year factor was included in the model regardless of its significance and, consequently, within year effects of the parameters are estimated. Tests of significance were based on deletion of the explanatory variable from the full model

									Year effect				
Parameter	*n*	Deviance null model	Deviance full model	Estimate	Delta deviance	d.f. 1	d.f. 2	*F*-value	*P*	Delta deviance	d.f. 1	d.f. 2	*F*-value	*P*
Mass (g)	38	52·26	49·77	–0·1133	0·07	1	34	0.05	> 0.80	2.32	2	34	0.79	> 0.4
Mass change (g)	34	47.02	38.95	–1.936	4.87	1	30	3.75	> 0.60	3.22	2	30	1.24	> 0.3
Condition (g)	38	52.26	49.37	–0.3159	0.47	1	34	0.33	> 0.50	2.29	2	34	0.79	> 0.4
Working day (h)	31	42.17	32.31	–1.007	2.72	1	27	2.27	> 0.14	6.19	2	27	2.59	> 0.09
Visits (number/day)	36	49.46	40.42	–0.01014	6.65	1	32	5.26	< 0.05	1.27	2	32	0.50	> 0.6
DEE (kJ/day)	38	52.26	44.95	–0.0584	4.90	1	34	3.70	> 0.06	3.31	2	34	1.25	> 0.2
DEE/BM (kJ/(day*g))	38	52.26	44.47	–1.107	5.37	1	34	4.11	> 0.05	3.53	2	34	1.35	> 0.2
Number of young	38	52.26	33.03	–0.5149	16.82	1	–	$\chi^2 = 16.82$	< 0.0001	1.50	2	–	$\chi^2 = 1.496$	> 0.4

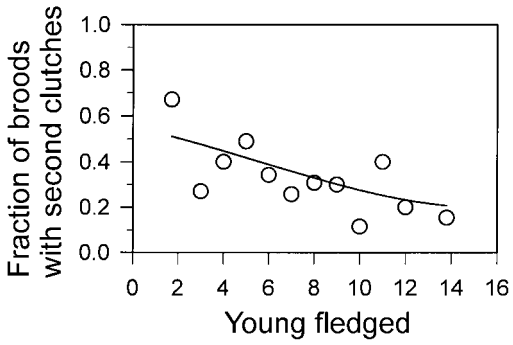

Fig. 6. The probability of a second clutch in relation to the number of young fledged from the first clutch. Line gives logistic fit to original data. Points represent means. $n \approx 30$ broods per point.

gories (Tukey pair-wise comparison, $P < 0{\cdot}02$, log transformation to equalize variances). Nestling condition was negatively related to manipulation ($F_{1,222} = 53{\cdot}11$, $P < 0{\cdot}001$) and did not differ between years ($F_{4,218} = 1{\cdot}832$, $P > 0{\cdot}12$).

As mentioned, the probability of a second clutch was strongly dependent on manipulation. When manipulation was accounted for, an additional effect of the number of fledglings was found ($\chi^2 = 5{\cdot}96$, d.f. $= 1$, $P < 0{\cdot}05$) and manipulation could be deleted from the model ($\chi^2 = 1{\cdot}56$, d.f. $= 1$, $P > 0{\cdot}2$). The number of fledglings was thus a more powerful explanatory variable regarding the probability of birds laying a second clutch (Fig. 6; $\chi^2 = 18{\cdot}48$, d.f. $= 1$, $P < 0{\cdot}0001$). No additional effect of nestling mass or condition could be found ($\chi^2 < 0{\cdot}05$, d.f. $= 1$, $P > 0{\cdot}8$). The absence of a mass/condition effect is not due to co-linearity between number of fledglings and nestling mass/condition, because removal of fledgling number from the model did not change the result.

Relative impact of parents and brood

In the previous sections, the effects of brood state and parental state on the probability of a second clutch were analysed independently, and combined analysis could change the result because of increased power. However, parental mass, tarsus or condition did not significantly explain additional variance if included in the model containing year, birth date of young and number of fledglings (all $\chi^2 > 1{\cdot}68$, d.f. $= 1$, $P > 0{\cdot}19$). Using the restricted data set we extended this analysis and tested whether in addition to the brood size effect, the effect of the other variables could reduce the explained variance significantly. This was not the case, the number of young in the nest alone was the variable that explained the variance (Table 2). Other variables did not explain significantly more variation in combination with the brood size effect.

Discussion

The main findings of this study were that: (i) brood size manipulation affected parental condition (ii) females rearing reduced broods had a lower feeding rate and DEE_{fem}, whilst brood enlargement had no effect on these measures; females reached an energetic ceiling similar to that of natural brood sizes (iii) the level of the energetic ceiling differed between years, and finally (iv), there was no consistent association between our measures of parental effort (DEE_{fem}, feeding rate, condition) and the costs of reproduction.

CONDITION

When parents were weighed during the day, there was a negative relationship between manipulation and condition in both sexes (Fig. 2). The relationship between brood size manipulation and parental mass (loss) in great tits was previously studied by Smith *et al.* (1988), Lindén (1990) and Verhulst & Tinbergen (1997), with results differing between studies. However, when the results from these studies are pooled by calculating the weighted mean correlation coefficient (following Hedges & Oilkin 1985; pp. 230–232), it emerges that, on the whole, a negative association between parental mass/condition and brood size manipulation is found in both sexes (males: $r = -0{\cdot}12$, $n = 503$, $P < 0{\cdot}006$; females: $r = -0{\cdot}16$, $n = 549$, $P < 0{\cdot}0003$). Thus, we conclude that, on average, great tits respond to a brood size manipulation with a change in mass, at least during the day.

Although a negative effect of brood size manipulation on female mass was found when birds were measured during the day (nestling age 8), in our study female mass measured at night (nestling age 12), was not related to manipulation (Fig. 2a). Since both time of day and nestling age differ between the two measurements, in principle either (or both) could be involved in explaining this discrepancy. If we assume that the difference between day and night condition is fixed, thus independent of nestling age and manipulation, the results suggest that female condition decreases in dependence of manipulation early in the nestling period towards a common level, independent of manipulation, later in the nestling period. An alternative explanation of the observed pattern is that manipulation affects the difference between the day and the night measurements. The discrimination between these two hypotheses requires mass measurements during day and night over a range of nestling ages for manipulated broods.

A functional interpretation of the negative association between brood size manipulation and parental mass is that reduced mass results in lower flight costs (Norberg 1981). As a consequence, birds with

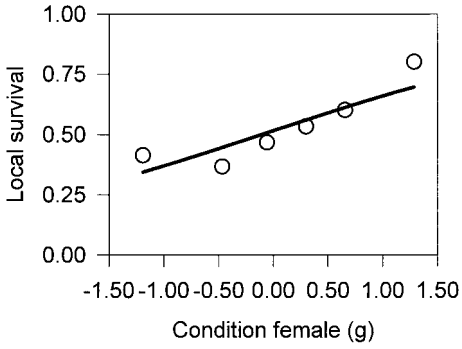

Fig. 7. Female local survival till next breeding season as a function of body condition at night 11 (logistic regression: $\chi^2 = 6{\cdot}10$, d.f. $= 1$, $P < 0{\cdot}02$; controlled for year: $\chi^2 = 14{\cdot}95$, d.f. $= 4$, $P < 0{\cdot}005$; deviance final model 230·70, d.f. $= 178$). Line gives logistic fit to original data, $n \approx 30$ birds per point.

enlarged broods could allocate a larger share of their foraging yield to the brood. However, this is unlikely to be the whole story, since it does not explain why parents rearing reduced broods do not also reduce their mass. From a simple optimality perspective, it appears that there are apparently costs associated with reducing mass, which make it suboptimal for females rearing reduced broods to reduce their mass. The nature of these costs remains unclear however, because we found no association between day 8 condition and the costs of reproduction. Further analysis shows that female winter survival was also independent of day 8 condition ($\chi^2 = 0{\cdot}33$, d.f. $= 1$, $P > 0{\cdot}5$, controlled for year). In contrast, however, condition on night 12 was correlated positively with winter survival (Fig. 7 $\chi^2 = 7{\cdot}03$, d.f. $= 1$, $P < 0{\cdot}01$, controlling for year). Condition on night 12 may thus have an important biological meaning. As shown, the condition on night 12 was not affected by manipulation, which is consistent with the fact that we found no survival effects of manipulation (Tinbergen & Daan 1990). Thus, in contrast to the results of Nur (1984a, 1984b; but see Pettifor 1993), we cannot interpret the association between condition and survival in terms of manipulation effects.

EFFORT

The effect of brood size manipulation on feeding rates has previously been studied in great tits (Smith *et al.* 1988; Verhulst & Tinbergen 1997; with only control and reduced broods), and our results are consistent with these studies (i.e. a reduction in reduced broods and no effect of brood enlargement). A ceiling to feeding rate is not uncommon: 24% of species that reduced their feeding rate in response to brood reduction did not increase their feeding rate when the brood was enlarged ($n = 17$ species, including the great tit; calculated from Table 2 in Lessells 1993). It is consistent with the results on feeding rate that DEE_{fem} also levelled off with brood size (Fig. 4), although this pattern contrasts with our findings in the great tit population on Vlieland, where brood size reduction did not result in a decrease in DEE_{fem} (this contrast is further discussed in Verhulst & Tinbergen 1997).

The DEE_{fem} of the birds that did not sleep the second night in their nest box was related more strongly to ambient temperature than the DEE_{fem} of females that did sleep in their nestbox (Fig. 1). This suggests that the temperature effect acts, at least partly, during the night. Other studies of free-living birds also concluded that temperature is an important source of variation in DEE (Tatner 1990; Mock 1991; Sullivan & Weathers 1992; Dykstra & Karasov 1993). Since the ambient temperature had a substantial effect on DEE (Fig. 5a), it follows that energy expenditure as an estimate of parental effort of a great tit bears no simple relationship to feeding rate. This is further illustrated by the fact that it varies between species whether or not feeding rate correlates with DEE at all (Bryant 1988), and by the fact that DEE_{fem} did not correlate with feeding rate of female great tits in another population (Verhulst & Tinbergen 1997).

Energy expenditure per gram body mass may potentially be a more relevant parameter to estimate effort than whole body metabolism, when energy turnover per gram of tissue determines the costs of reproduction. Therefore, we repeated the analyses using DEE_{fem} divided by female body mass. DEE_{fem}/BM differed between years and, again, inter-annual variation could be explained by the temperature effect. DEE_{fem}/BM also depended on the manipulation, but in contrast to DEE_{fem}, not on its square. However, at this point the results depended critically on the selection of the data. When those females that did not spend both nights in the nest box were excluded ($n = 10$, see Methods), both DEE_{fem} and DEE_{fem}/BM showed a significant curvilinear relationship with manipulation (effect manipulation squared controlled for manipulation and year: DEE_{fem} $F_{1,23} = 19{\cdot}13$, $P < 0{\cdot}001$; DEE_{fem}/BM $F_{1,23} = 8{\cdot}748$, $P < 0{\cdot}01$). Since this data selection constitutes the most homogeneous data set, we tentatively conclude that an energetic ceiling also exists on DEE_{fem}/BM. This is consistent with our results on Vlieland, where DEE_{fem} apparently already reached an energetic ceiling when rearing reduced broods and this pattern also did not change when using DEE_{fem}/BM (Verhulst & Tinbergen 1997).

PARENTAL EFFORT AND FITNESS

We set out this study to investigate the importance of DEE in causing the costs of reproduction, as sug-

gested for the Kestrel *Falco tinnunculus* in which Deerenberg and co-workers (Deerenberg *et al.* 1995; Daan, Deerenberg & Dijkstra 1996) found a negative correlation between DEE and survival until the next breeding season. However, our finding that brood enlargement caused a cost of reproduction, but did not increase DEE_{fem}, refutes DEE_{fem} as a cause for the cost of reproduction. We previously reached the same conclusion for another great tit population, where brood size reduction also revealed a cost of reproduction, while there was no experimental effect on DEE_{fem} (Verhulst & Tinbergen 1997). Consequently, the work level could not be explained as a balance between fitness costs and benefits related to energy expenditure. The number of young after manipulation was the best predictor for the cost of reproduction in the present study, but since provisioning rate, DEE_{fem}/BM and the number of young after manipulation were correlated ($r > 0{\cdot}52$), the interpretation of their separate roles remains somewhat ambiguous. Nevertheless, we judge it unlikely that DEE is a general predictor for fitness consequences of effort.

THE ENERGETIC CEILING

The results in this paper (Fig. 4) clearly point at an energetic ceiling (*sensu* Drent & Daan 1980), but not at a fixed ceiling: within years the average great tit female reduced her energy expenditure for reduced broods, yet did not spend more energy to provision the enlarged broods. To our knowledge, this is the first demonstration of such an 'energetic ceiling' in nature.

When discussing factors that might impose metabolic ceilings, Hammond & Diamond (1997) distinguished between limitations imposed by properties of the animals' body (energy-consuming and/or energy-supplying machinery) or by food availability. However, in a natural situation, a limit on food availability may be imposed by a limit in the available foraging time. Since there are a great number of ecological factors that affect foraging time (daylight period, tidal cycle, prey behaviour), we propose to broaden the suggestion of Hammond & Diamond (1997), and distinguish extrinsic (ecological) factors causing an energetic ceiling from intrinsic factors (body properties).

This raises the question whether the energetic ceiling that we observed was determined by the intrinsic or extrinsic factors. The ceiling at which females worked was around 3·3 times BMR, close to the average reported for birds at this reproductive phase (3·1–3·6 times BMR, Daan, Masman & Groenewold 1990b; Peterson, Nagy & Diamond 1990; Bryant & Tatner 1991), but relatively low for a maximum sustained level of energy expenditure according to Hammond & Diamond (1997; 4·3–6·7 times RMR and RMR is usually higher that BMR). Furthermore, Lindström & Kvist (1995) reported that the maximum rate of energy assimilation in birds was around 4·6 times BMR, substantially higher than 3·3 BMR. Dykstra & Karasov (1993) showed that, in the house wren (*Troglodytes aedon*), the near maximum rate of energy expenditure (measured in the laboratory using forced exercise and cold stress) was well above field energy expenditure during chick rearing. From this and the fact that there was no relationship between brood size and parental energy expenditure they concluded that brood size was unlikely to be limited by intrinsic factors. Lastly, and perhaps most importantly, the idea of a single 'energetic ceiling' imposed by intrinsic factors is at variance with the annual differences in the level of the DEE_{fem} asymptote in this study (Fig. 4). These observations suggest that the ceiling on DEE_{fem} was imposed by extrinsic factors.

What extrinsic factor could have limited DEE_{fem}? Our analysis suggests that the annual level of the energetic ceiling was related to ambient temperature, but the number of years available to evaluate this point was small. It is worth noting, therefore, that we previously observed annual variation in great tit DEE_{fem} in the Vlieland population (Verhulst & Tinbergen 1997), and also in this data set the year effect was no longer significant ($F_{2,27} = 0{\cdot}68$, $P = 0{\cdot}5$) when ambient temperature was controlled for ($b = -2{\cdot}78$ kJ/°C, SE $= 1{\cdot}16$, $F_{1,27} = 5{\cdot}79$, $P < 0{\cdot}025$; S. Verhulst & J. M. Tinbergen, unpublished). This lends further support to the suggestion that annual variation in DEE_{fem} was caused by variation in ambient temperature.

Although ambient temperature may explain variation in the annual level of the energetic ceiling, this does not yet explain why there is a limit on DEE_{fem} in the first place. A temperature-dependent limit to energy expenditure, perhaps due to heat stress during work, would provide a link between ambient temperature and an energetic ceiling. However, on the basis of this hypothesis we would predict lower female feeding rate at higher temperatures, which was not the case ($P > 0{\cdot}6$), leading us to reject this possibility.

In our study a very large part of the daylight period was spent feeding young and it is therefore not surprising that pairs rearing enlarged broods did not spend more hours per day feeding their brood. If it can be assumed that energy expenditure while foraging was independent of manipulation, time limitation seems the most straightforward explanation of the energetic ceiling in the great tit. In this view, control birds already worked the full day and brood enlargement did not change this, while brood reduction led to free time. The fact that we did not find differences between manipulation categories in the number of active hours per day suggests that this

free time was taken up in the course of the day, which may well be optimal from the perspective of the young. In a great tit population in Finland, with a much longer daylight period (natural) variation in brood size was positively correlated with length of active day and DEE_{fem}, which also correlated with each other (Sanz *et al.* 1998). Although brood size manipulation experiments are required to verify these results, this study does provide some support for the time-limitation hypothesis, since it shows that DEE_{fem} increases with brood size under conditions where day length does not limit parental effort.

THE ENERGETIC CEILING AND FITNESS

It is important to realize that when discussing the extrinsic and intrinsic limitations setting an energetic ceiling, we are confining ourselves to proximate explanations. Alternatively, fitness costs could increase disproportionally near to the observed energetic ceiling, in which case birds would simply not be motivated to work harder for the enlarged broods, because of the disproportional increased fitness costs this would entail. With the present data we cannot distinguish between the proximate and functional explanations. Furthermore, they are probably not independent, in the sense that the metabolic rate that can be sustained without great fitness costs would undoubtedly be evolutionary adjusted to any external limitations that impose themselves with high frequency.

We originally set out this study to quantify the fitness costs associated to parental energy expenditure in the great tit, in order to estimate the optimal energy expenditure. However, we did not find convincing evidence that energy expenditure bears a fitness cost in this system (see above). In more general terms we expect that, whether time limited or not, reallocation of energy as a consequence of changing brood demands is a general phenomenon and potentially takes place over many dimensions. Data are accumulating that birds with a high work load reduce night expenditure (Bautista *et al.* 1998; Deerenberg *et al.* 1998) and may allocate less resources to immune function (Sheldon & Verhulst 1996; Deerenberg *et al.* 1997; Nordling *et al.* 1998). Thus, we agree with Bryant (1988) that it is unlikely that, as a general rule, the rate of energy expenditure alone could serve as shortcut to estimate the cost of reproduction.

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